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Comparison of cranial ontogenetic trajectories among great apes and humans

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Abstract

Molecular data suggest that humans are more closely related to chimpanzees than either is to the gorillas, yet one finds the closest similarity in craniofacial morphology to be among the great apes to the exclusion of humans. To clarify how and when these differences arise in ontogeny, we studied ontogenetic trajectories for *Homo sapiens*, *Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla* and *Pongo pygmaeus*. A total of 96 traditional three-dimensional landmarks and semilandmarks on the face and cranial base were collected on 268 adult and sub-adult crania for a geometric morphometric analysis. The ontogenetic trajectories are compared by various techniques, including a new method, relative warps in size–shape space. We find that adult *Homo sapiens* specimens are clearly separated from the great apes in shape space and size–shape space. Around birth, *Homo sapiens* infants are already markedly different from the great apes, which overlap at this age but diverge among themselves postnatally. The results suggest that the small genetic differences between *Homo* and *Pan* affect early human ontogeny to induce the distinct adult human craniofacial morphology. Pure heterochrony does not sufficiently explain the human craniofacial morphology nor the differences among the African apes.

Keywords: Allometry; Cranial morphology; Geometric morphometrics; Heterochrony; Hominid evolution; Ontogenetic divergence; Size–shape space

Introduction

Over the last few years the discrepancies among hominid[1] classifications based on molecular and morphological data have fuelled the debate on one of the most controversial and persistent problems

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[1] Taxonomy according to Mann and Weiss (1996). Hominidae include humans and great apes.

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in paleoanthropology: the precise relationship of humans to our closest living relatives, the great apes. Molecular data suggest that humans are more closely related to chimpanzees than either is to the gorillas, yet one finds the closest morphological similarity to be among the great apes to the exclusion of humans (Man and Weiss, 1996; Ruvolo, 1997; Enard et al., 2002; Kaessmann and Pääbo, 2002). The human cranium possesses a morphology quite distinct from that of *Pan*, while one recent molecular study (Wildman et al., 2003) even supports the old attempt to place chimpanzees within the genus *Homo*.

The genetic difference between *Homo* and *Pan* comprises the accumulation of point mutations as well as chromosomal rearrangements, but Pääbo (1999) suggests that neither is likely to cause the majority of species-defining phenotypic differences. Instead he stresses the importance of changes in the structure or expression of a few genes that exert effects either during development or in adulthood. As it is difficult to study gene expression on a molecular level for the whole organism, we confine ourselves to the study of the morphological *effects* of gene expression during ontogeny. The analysis of morphological patterns and results in terms of underlying processes, or shifts in the parameters controlling development, offers a potential link between morphology and genetic regulation (Alberch et al., 1979). We assess the appearance of these differences in cranial morphology during ontogeny using a sample of dried skulls of modern humans and great apes ranging from newborn to adult specimens. Applying the toolkit of geometric morphometrics (Bookstein, 1991; Marcus, 1996; Dryden and Mardia, 1998) we construct a shape space where the landmark configuration of each specimen is represented by a single point. Within this space, the ontogenetic sequence of specimens belonging to one species is called an ontogenetic trajectory. The development of different species can thus be compared by geometric contrasts among their ontogenic shape trajectories (Klingenberg, 1998; O'Higgins, 2000a,b).

It was von Baer (1828) who first stated that related species share their early embryogenesis, but independently develop specialized features in later ontogeny. In modern comparative embryology, this traditional idea has been superseded by the concept of phylotypic stage (Sander, 1983; Slack et al., 1993; Raff, 1996; Hall, 1997) or phylotypic period (Richardson, 1995): Early development, however different, converges to a highly conserved stage (namely, the phylotypic stage) midway through embryological development, and diverges thereafter in later ontogeny to produce distinct adult morphologies (Richardson, 1999). This concept is commonly referred to as the "developmental hourglass". For vertebrates the phylotypic stage starts approximately with neurulation and ends when most of the somites have been formed (Galis and Metz, 2001). Though recent studies fundamentally question the general applicability of the phylotypic notion for vertebrate evolution (Richardson et al., 1997; Richardson, 1999; Bininda-Emonds et al., 2003), these critics continue to assume that in a monophyletic clade the concept of a phylotypic stage may be seen as a valid generalization about common patterns of organogenesis (Richardson, 1999).

Schultz (1924) was the first to show that prenatal and infantile primates are much more similar than adults and that human evolution should be studied in terms of these diverging growth processes. Applying multivariate morphometrics, Richtsmeier et al. (1993) demonstrate for three primate species that though their facial shape is already distinct in infancy, postnatal growth contributes significantly to adult morphology. In shape space this corresponds to ontogenetic trajectories of related species being rather similar in early development and subsequently diverging. Geometric morphometric studies on different primate species (O'Higgins, 2000a,b; O'Higgins et al., 2001) confirm this assumption. Recent geometric morphometric studies of hominid craniofacial growth (Ponce de Leon and Zollikofer, 2001; Ackermann, 2002; Penin et al., 2002), however, all find different but more or less parallel trajectories in shape space from dental stage I (eruption of first permanent molar) to adulthood. It follows that within hominids the ontogenetic development of cranial morphology must diverge from that of the other apes in early postnatal or prenatal ontogeny. To yield additional insight into this divergence

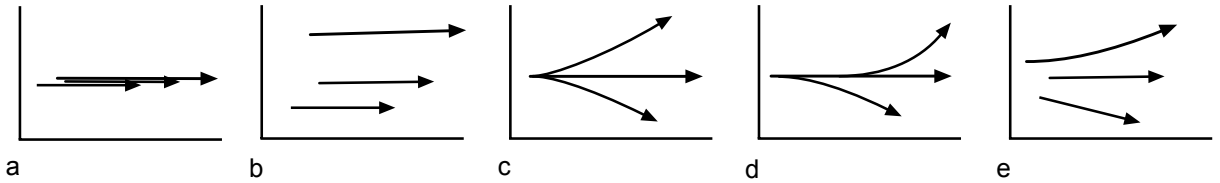

Fig. 1. Sketch of possible patterns of three different postnatal ontogenetic trajectories in shape or size–shape space. In studies of shape space, the horizontal axis is generally "allometric shape", the pattern of shape predicted by regression on size; in studies in size–shape space, this axis is variously geometric or allometric size itself. The vertical axis will usually be a composite shape measure computed to optimize some sort of statistical summary.

of hominid ontogeny, the present study uses a large number of landmarks and semilandmarks (Bookstein, 1997; Gunz et al., in press) measured on specimens from a few days after birth on.

One classic approach to the study of ontogeny and phylogeny is "heterochrony", the dissociation of size, shape and age (Gould, 1977; Alberch et al., 1979). In this approach, shape—as a proxy for development—is always measured by a single shape variable (usually a size ratio). The focus of our multivariate analysis, however, is a more general dissociation of growth patterns, which includes the *dissociation of growth and development* (i.e., size and shape) and the *dissociation of regional growth fields* (categories recognized by Gould in 1977). The dissociation of regional growth fields subsumes *dissociated* or *mosaic heterochrony* (regional dissociation of temporal growth patterns; David, 1990; McKinney and McNamara, 1991), and also *heterotopy* (the change of *spatial* patterns of development sensu Zelditch and Fink, 1996). An *overall* dissociation of size and shape—i.e., pure heterochrony—results in identical trajectories in shape space but different associations with size (divergence in size–shape space, see below). Both kinds of *regional* dissociation of growth fields yield diverging shape trajectories (Godfrey and Sutherland, 1996) so that distinguishing between the concepts of mosaic heterochrony and heterotopy is not possible in an overall multivariate analysis of morphometric variables based on principal components or similar techniques (Bookstein et al., 1985; Mitteroecker et al., in press). We center our analysis of the five hominid species on the basic temporal pattern of ontogenetic divergence, including dissociation both of size vs. shape and of regional growth fields.

Because we assume that postnatal ontogeny contributes considerably to adult inter-species differences in hominid craniofacial morphology, we expect diverging ontogenetic trajectories in the time frame investigated in the present study. Over any period of presumably homologous developmental stages, such as postnatal ontogeny, a set of ontogenetic trajectories can exhibit several principal patterns of divergence (Fig. 1):

a. Trajectories may not diverge at all in shape space, so that the species investigated undergo one single series of shape changes during development. This is the only context to which the classic terminology of heterochrony applies (i.e., these shape changes occur at different sizes or ages). If, instead, the trajectories diverge in shape space, no valid description of changes in allometry is possible that is not specific by region, and so the concept of overall heterochrony should not be used (Bookstein et al., 1985; Godfrey and Sutherland, 1996; Zelditch and Fink, 1996; Mitteroecker et al., in press).
b. Trajectories may be parallel, so that all of the divergence from some common ontogeny appears prior to the age of the youngest specimens. This was the case in the geometric morphometric studies on hominids cited above.
c. There may be a common "point of divergence" for some or all species, after which they diverge at more or less different rates.
d. Trajectories may diverge from the common ontogeny at different points in shape space or

size–shape space. The species diverging earlier in their ontogeny from the common line likely differ more fundamentally from the others in their adult morphology (von Baer, 1828; Gould, 1977; Raff, 1996; Wimsatt, 1996; Richardson, 1999).

e. Trajectories may be skewed, indicating no clear pattern of divergence in the observed time range.

It is not clear *how* and *when* the cranial differences between *H. sapiens* and the great apes emerge during ontogeny. We state three specific hypotheses:

H_1: Pure heterochrony. Human adult cranial form is retarded along a shape trajectory that is common with the apes (Fig. 1a). Shape and size could be retarded jointly ("ontogenetic scaling", Shea, 1981, 1983a,b), or a dissociation may have occurred. The hypothesis that human morphology is neotenic, i.e., that it possess a paedomorphic shape at the same or higher size and age of maturation with respect to ancestral morphology (usually inferred from chimpanzee morphology), has a long history (e.g., Bolk, 1926; De Beer, 1951; Pilbeam and Gould, 1972; Gould, 1977; Montagu, 1989). However, there are many counterarguments and methodological critiques against the claim of a single neotenic process (Dean and Wood, 1984; Bromage, 1985; Bogin, 1999; Shea, 1989; McKinney and McNamara, 1991; Vrba, 1994; Godfrey and Sutherland, 1996; Wood, 1996). Also, more recent geometric morphometric studies (Penin and Berge, 2001; Ackermann, 2002; Penin et al., 2002) find different ontogenetic trajectories for *Homo* and great apes. Pure heterochrony of human cranial growth relative to *Pan* is an inappropriate description if the ontogenetic trajectories are not identical in shape space.

Among many possible hypotheses alternative to H_1, the following two are of greatest interest:

H_2: Human ontogeny may diverge at a developmental stage similar to that at which the great apes diverge among themselves (Fig. 1c). Humans would then reach their distinct morphology by having a relatively steeply diverging ontogenetic trajectory.

H_3: Alternatively, human ontogeny may deviate relatively earlier from common ontogeny than do the great apes (Fig. 1d). This early divergence of trajectories could account for the markedly different morphology of humans and great apes because early changes in development usually have a high impact on later ontogeny and adult form ("amplification", see Arthur, 1997; Richardson, 1999).

Especially in growth studies, size is of direct biological interest. Though shape space omits information on overall scale (Bookstein, 1991; Rohlf, 1996), description and comparison of development can also be made in size–shape space (Dryden and Mardia, 1998). Two species at the same developmental stage could have the same shape at different sizes or different shapes at the same size. In this paper we include geometric size in the analysis so that differences or divergences of allometry can be assessed at the same time as differences or divergences of ontogenetic shape (Mitteroecker et al., in press).

Material and methods

Data

For this study we used 268 crania (206 adults and 62 sub-adults) of five different hominid species: *Homo sapiens*, *Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*. The specimens are approximately equally distributed across species and sex (Table 1) and the ages span the full range from perinatal/early postnatal stages to adulthood. The youngest specimens from each species are approximately of the same age. Except for several infants, all ape specimens are wild-shot. The human sample was selected to cover a wide range of morphological variability. Age was estimated by dental eruption pattern for the older specimens and was known exactly for most infants (for more details see Bernhard, 2003).

Three-dimensional coordinates of 41 homologous ectocranial anatomical landmarks (Table 2) on the face and cranial base together with five ridge curves (Table 3) on the left side of every cranium were digitized using a Microscribe 3DX. The measurements were taken by a single person

Table 1
Number of specimens for each species and sex

	Adults		Subadults		Collection*
	Female	Male	Female	Male	
Pongo pygmaeus	24	23	5	5	1, 2
Pongo pygmaeus pygmaeus	23	22	5	5	
Pongo pygmaeus abelii	1	1	–	–	
Gorilla gorilla gorilla	21	23	6 (1)	6 (4)	2,3
Pan troglodytes	19	20	6 (2)	4	2, 3, 4
Pan troglodytes troglodytes	14	14	1	4	
Pan troglodytes schweinfurthii	0	3	1	–	
Pan troglodytes verus	5	3	2	–	
Pan paniscus	20	16	6	6	4
Homo sapiens	20	20	7	11	
South and Sub-Saharan Africa	–	4	–	–	5, 6
Asia	8	8	–	–	5, 6
South America	–	4	–	–	5, 6
South-East and Central Europe	12	4	7	11	6, 7

*Collection codes: 1=State Collection for Anthropology and Palaeoanatomy, Department of Anthropology, Munich, Germany; 2=First Zoological Department of the Natural History Museum, Vienna, Austria; 3=Institute of Anthropology, University of Zuerich-Irchel, Switzerland; 4=Royal Museum for Central Africa in Tervuren, Belgium; 5=Department for Archaeological Biology and Anthropology, Natural History Museum, Vienna, Austria; 6=Institute for Anthropology of the University of Vienna; 7=Institute of Anatomy, Medical University of Vienna. Numbers in brackets, when subspecies in not determined.

(M.B.) in two separate sessions per skull because not all landmarks could be reached in one orientation. The two sets of landmarks were fitted together by superimposing five fiducial points that were measured in both sessions. Along the curves a total of 55 equidistant semilandmarks per skull were placed and allowed to slide along their curves so as to minimize the net bending energy of the data set as a whole around its own Procrustes average. For statistical analysis, these relaxed semilandmarks can be treated as homologous within the sample (Bookstein, 1997; Bookstein et al., 1999; Gunz et al., in press). Because in many forms the neurocranium is concealed beneath a sagittal crest, we have omitted landmarks in that region.

Analysis of size and shape

The topic of this paper, the comparative study of allometry, has a long and rich history of biometric method. Among the many useful approaches to this topic are principal component (PC) analysis (Jolicoeur and Mosimann, 1960; Blackith and Reyment, 1971), regressions of Procrustes shape coordinates or relative warps on size (Bookstein, 1991), and other possibilities. In systematic applications, the methodological problem has generally been to separate empirical differences of morphological form among taxa into that part that is a consequence of size differences according to an allometric model, versus that part that is not (Bookstein et al., 1985). The separation is followed by analysis of these two parts separately (e.g., Burnaby, 1966, or "sheared principal components analysis"; Bookstein et al., 1985; or Rohlf and Bookstein, 1987). While in an ontogenetic sample consisting of only one species the first PC usually is the allometric shape component, this is rarely the case in a multi-species sample. The first PC will instead combine the "common" direction of growth with some interspecies shape differences

Table 2
Landmarks: traditional landmarks are defined in White (1991). Landmarks in italics were treated as semilandmarks in analysis. Nos. 1–13 are midline points. Nos. 14–28 are bilateral points and were measured on both sides

No.	Landmarks
1	prosthion
2	nasospinale
3	rhinion
4	nasion
5	glabella
6	opisthion
7	basion
8	sphenobasion
9	hormion
10	staphylion
11	intersection of medial and lateral palatal sutures
12	foramen incisivum
13	orale
14	point where the nasomaxillary suture meets the nasal aperture
15	intersection of nasomaxillary and frontonasal suture
16	maxillofrontale
17	zygoorbitale
18	frontomalare orbitale
19	zygomaxillare
20	zygion
21	mastoidale
22	auriculare
23	most superior point on the suture that separates zygomatic and perietal bone
24	*jugale*
25	frontomalare temporale
26	frontotemporale
27	point on the most posterior end of the alveolar ridge
28	*canine base*

and divergences. In this case, the "common allometry" is better estimated by a pooled regression of the shape variables, corrected for their species mean, on size (see Appendix). The scaled vector of regression slopes, which we call the *common allometric component* (CAC), can serve as the first principal direction of an ordination for which a PCA of the regression residuals supply subsequent directions of interest. This rotation of the original PC's does not affect the pattern of divergence between the growth trajectories, but matters for the success of visualization. Whereas CAC is an estimated factor, the subsequent PC's of residuals are statistical components without any necessary biological meaning of their own.

In this paper we wish to introduce a new method, not for the purpose of superseding any of the old methods but instead for the quite different purpose of embracing them all. We will show that one straightforward principal component analysis of the distribution of a landmark or semilandmark data set in size–shape space permits the reconstruction of all of the predecessor methods simply by varying the visualization. Most previous approaches to allometry, in this context of application to Cartesian coordinate data, thus emerge as special views of a single composite analysis from which multiple and subtle conclusions can be drawn.

This composite approach consists of a relative warp analysis not of the usual matrix of Procrustes shape coordinates (Bookstein, 1991; Rohlf, 1993) but instead of the matrix of those coordinates augmented by one single additional column for the logarithm of Centroid Size (CS). Thus we propose analysis of allometry by *principal components analysis of the empirical data distribution in size–shape space*, followed by multiple overlapping interpretations. Typically, log CS will have by far the largest variance of any column of this matrix, and thus the first principal component of the size–shape distribution will be closely aligned with size; but that is exactly analogous to the familiar fact that in any other allometric data set, the first principal component of any set of size-loaded measures is likewise very highly correlated with size however measured (Jolicoeur and Mosimann, 1960).

From this single principal component analysis, scientific insights arise via high-dimensional scatter plots of the resulting component scores, followed by free rotation of those scatters to orientations that correspond to the standard biological interpretations of the earlier literature. The rotated scatters are interpreted in words, while the rotation itself results in linear combinations of the principal components into new linear combinations of the original data that can be graphed by the usual method of thin-plate splines (now with size included in some circumstances).

We will refer to these components as SSPC1, SSPC2, …, where "SS" stands for "size–shape."

Table 3
Ridge curves

Curve	Description
Alveolar curve	a line following the outer alveolar margin (prosthion, canine base, postalveolare)
Nasal aperture	a line along the left margin of the nasal aperture, from rhinion to nasospinale (rhinion, pseudoalare, nasospinale)
Orbital rim	a line following the inner orbital rim (maxillofrontale, zygoorbitale, frontomalare orbitale)
Torus superciliaris	a line from glabella along the torus supraorbitalis to the point defined as frontomalare temporale (glabella, frontomalare temporale)
Upper zygomatic curve	a line starting at auriculare, following the upper edge of the zygomatic process to jugale, then along the temporal line to frontotemporale (auriculare, upper zygomatic, jugale, frontomalare temporale, frontotemporale)

Principal components that arise from other manipulations of the data will be defined by other acronyms: principal components of just the Procrustes shape variables will be called RW1, RW2, … (relative warps), and principal components of the residuals of shape coordinates after size is regressed out will be called RSC1, RSC2, … (residual shape components).

Visualization

We visualize growth trajectories as *scores* along the components described above—representing *temporal* patterns of shape change—and also as regionalized shape deformations representing *spatial* patterning (Bookstein, 1991; O'Higgins, 2000a,b). Biological interpretations based on two-dimensional scatter plots of PC scores can be influenced by the choice of projection of a higher dimensional phenomenon onto two dimensions. We try to minimize this effect by projecting reasonable rotations of the first three components of the data decomposition. This gives us a much better chance to understand the complex pattern of trajectories in their high-dimensional space (see also Oxnard, 1983). The 3D graphs are isometric—their axes are equally spaced—but due to the rotation they can appear foreshortened when printed.

We visualize spatial patterns by the effect of the corresponding thin plate spline on the triangulated surface from one single chimpanzee specimen (chosen because the chimpanzees lie close to an average morphology in this list of five taxa). This was done in the software package Edgewarp3D (Bookstein and Green, 2002). The surface information was extracted from a CT scan. The interpretation is of large-scale features only. All the morphometric and statistical software was programmed in MATHEMATICA®.

Results

Ontogeny in shape space

We performed a decomposition of Procrustes shape variables into a common allometric component (CAC) and a first residual shape component (RSC1). Figure 2 shows a scatter of RSC1 against CAC in the spirit of an ordinary PC1–PC2 plot. RSC1 separates the humans from the African apes and the orangs, while chimpanzees and gorillas separate along the CAC component. During later development the trajectory of Pongo in this projection is nearly parallel to that of the African apes, but seems to have diverged earlier, perhaps in perinatal ontogeny. While later human ontogeny is likewise somewhat parallel to the apes' in this projection, their earlier development clearly is skew to this shared trend. The whole human growth trajectory is shifted to the left along this dimension of common allometric shape change. The sexual dimorphism that is clear in this plot is the subject of a separate paper (Schaefer et al., in press).

In the direction of increasing size, the common allometric component (Fig. 3a) consists of a

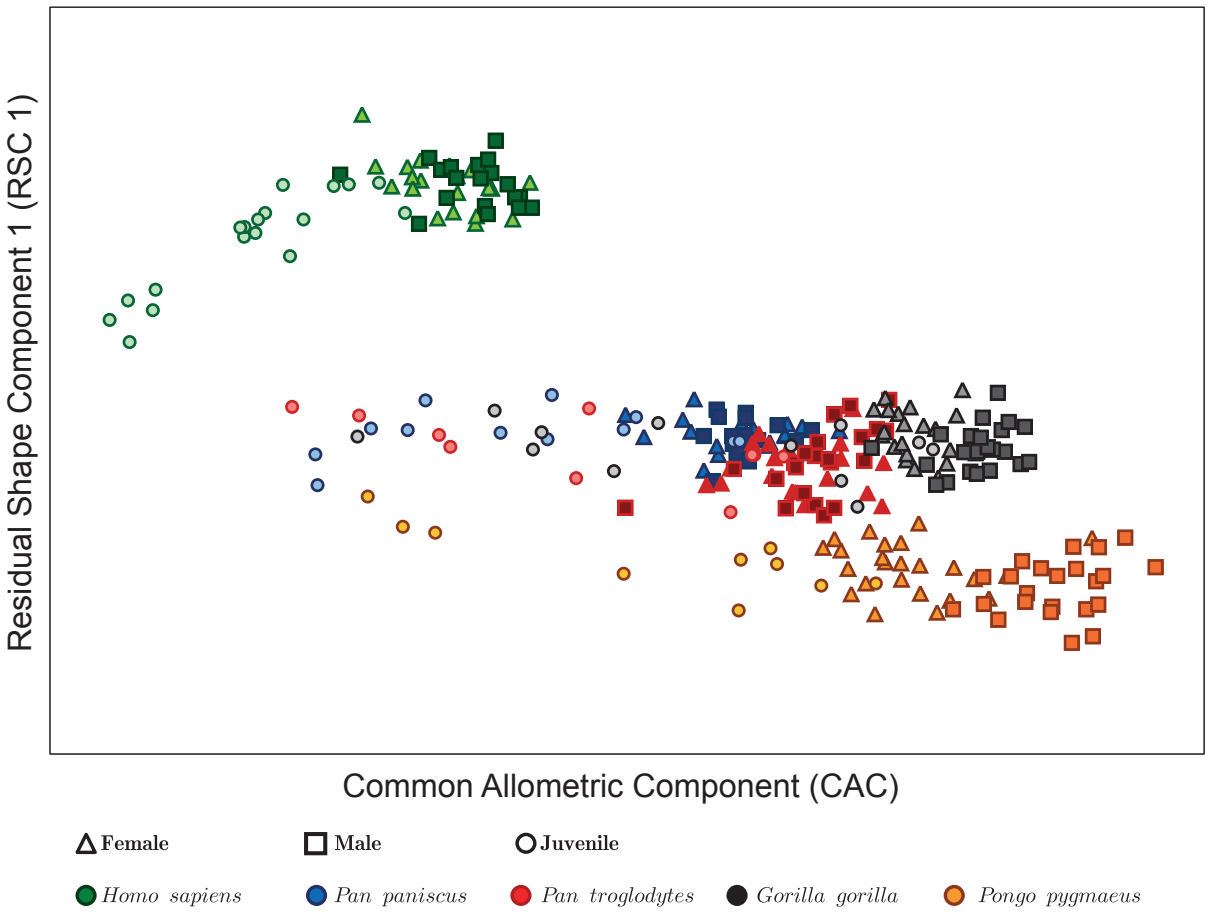

Fig. 2. CAC scores versus RSC 1 scores. The trajectories of the African apes overlap while humans and orangutans are clearly separate.

forward and downward growth of the maxilla and a decrease of orbital size and cranial base length relative to overall cranial size. The orbit changes from a rounded to a more rectangular shape and the occiput shifts slightly upward.

The shape differences associated with the residual shape component separating *Homo* from the African apes and *Pongo* are already manifest in the youngest forms we have (Fig. 2). As shown in Fig. 3b, RSC1 combines changes of orbital shape, an increase of inter-orbital distance, protrusion of the nasal bones, maxillary size, and the reorientation of the *foramen magnum* associated with flexion of the cranial base.

Allometric growth

As we mentioned earlier, divergences might appear in the relationship of allometric shape to size itself. These possibilities can be investigated by augmenting the CAC-RSC1 views by log CS. Figure 4 shows the strong linear correlation of scale with the common allometric component within all five species (all within-species r's are at least 0.92). The trajectory for *H. sapiens* is parallel to that in the apes, and begins at the same size at time of birth, but has lower shape scores (CAC axis). Thus human adult size is in the range of that of adult chimpanzees, while adult allometric shape

Fig. 3. (a) Morphs of a chimpanzee skull surface to illustrate the common allometric shape component (CAC). Left: smaller forms; right: larger forms. Shape deformations are arbitrarily magnified to ease interpretation. (b) First non-allometric shape component (RSC1). This analysis does not include landmarks on the teeth and therefore the surface morphs do not take into account dental changes.

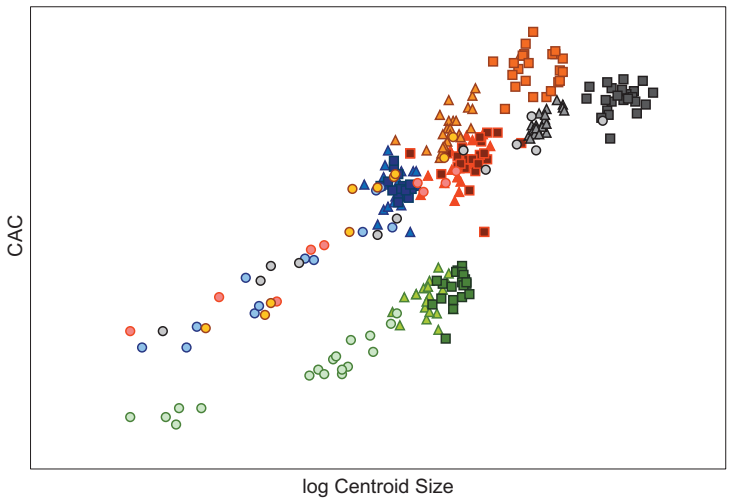

Fig. 4. Log centroid size plotted against the common allometric component scores by species. (The legend here and in all subsequent figures is as in Fig. 2.)

is comparable to that of the juvenile apes. The non-human species start at quite similar values of size and allometric shape. The African apes follow one single allometric vector, whereas the orangutans diverge before reaching adulthood, so as ultimately to achieve higher allometric shape scores than predicted for their size.

This plot resembles the classic size–shape plots of Alberch et al. (1979) for judging heterochrony. But since Fig. 2 reveals different trajectories in shape space, the concept of heterochrony cannot directly be applied to interpret this scatter plot in a formally and biologically consistent way. Recall that only when using a single shape variable, as in the majority of classic studies, can interpretation as heterochrony go forward. Also, Godfrey and Sutherland (1995a,b) have cautioned about the use of size as a proxy for age in heterochrony studies.

We find divergence of growth trajectories in all the previous plots linking CAC, RSC1, and centroid size. The pattern of divergence is thus at least a three-dimensional one and should be studied in the three-dimensional context of Fig. 5, from which all the previous conclusions follow by examination under rotation (Oxnard, 1983).

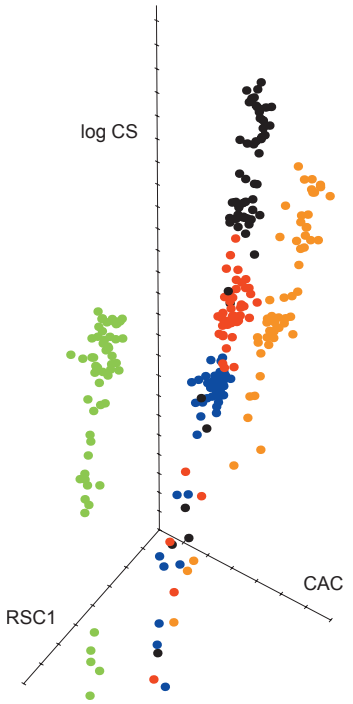

Fig. 5. CAC, RSC1, and size as a single three-dimensional space.

Size–shape space

As we noted in our methodological introduction (see also Appendix), the three-dimensional size–shape space of Fig. 5 could have been produced directly via plotting the first three principal components of the combination of the Procrustes shape coordinates with log CS. This combination is not geometric—we do not multiply the shape coordinates by size, or anything like that—but algebraic: the shape information is simply supplemented by size information and the whole PCA repeated. One advantage of this approach in contrast with that of Fig. 5 is that we gain resolution. Since the first PC of shape space usually is highly correlated with size, provision of axes for both variables is redundant. In size–shape space, allometric shape and geometric size both will be reflected in a single size–shape component, usually the first PC of this space.

Figure 6 shows three views of the scatter in this new space. The pattern of divergence strongly depends on the angle of view; arbitrary projections, such as those of Figs. 2 and 4, are not guaranteed to be meaningful. Because size (log CS) is a variable in the eigenanalysis, and because it dominates the first SSPC, we can draw it as a direction in this plot by reference to its loadings on the eigenvectors included. The magnitude of size allometry is indicated by the angles between the vector for CS and the direction of SSPC1, and the correlation of any score whatever on size is the cosine of the angle between the vector for CS and the selected direction in the full PC space (when scaled correctly). As shown in Fig. 6, this direction is more or less aligned with the long axes of all of the taxon-specific subscatters separately: a familiar finding, again, within this entire class of multivariate methods.

African apes

In Fig. 2 through Fig. 6 the African apes share a single ontogenetic trajectory and do not appear to diverge. When analyzing a second residual shape component (RSC2) this appearance changes (Fig. 7). The analysis can be focused in a different way by omitting the humans and orangutans and computing the first three components of size–shape space for the African apes alone. Figure 8 shows that the adult forms do not differ only by allometric scaling and that these differences appear mainly postnatally.

Discussion

In the components of shape space and size–shape space we have examined, the adult *Homo sapiens* specimens are clearly separated from all non-human adults (Figs. 2 and 5, and Fig. 6). However, the majority of molecular studies suggest close relationship of *Homo* and *Pan* to the exclusion of *Gorilla* (Man and Weiss, 1996; Ruvolo, 1997; Gagneux et al., 1999 but see also Deinard and Kidd, 1999; Barbulescu et al., 2001; Pääbo, 2003). Such an incongruence between morphological and molecular systematics is not uncommon within primates. Fleagle and McGraw (1999), Collard and Wood (2000), Singleton (2002) and Frost et al. (2003) discuss a similar inconsistency for papionins. After all, morphology, and especially craniodental morphology, is grounded not only in phylogeny but also in functional adaptations and convergence (Collard and Wood, 2000; Gibbs et al., 2000; Lieberman, 2000; Collard and O'Higgins, 2001). Oxnard (2000) notes that, whereas species separations, considered morphometrically, tend to relate to the function of anatomical parts separately, analyses of evolutionary relatedness tend to combine variables from several parts at once, and to make sense in terms of dynamic development rather than static adult form. Morphometric analysis, he notes, should always partition the two types of explanation. Our analysis addresses the ontogenetic realization of these morphological differences however they evolved.

The ontogenetic trajectories in the present study exhibit—as expected—a pattern of general divergence: the youngest specimens are much more similar than the adults. This means that within-species allometries are different and therefore the residual shape components (RSC) that result from partialing out pooled allometry still correlate with size *within most single species*. A similar pattern of

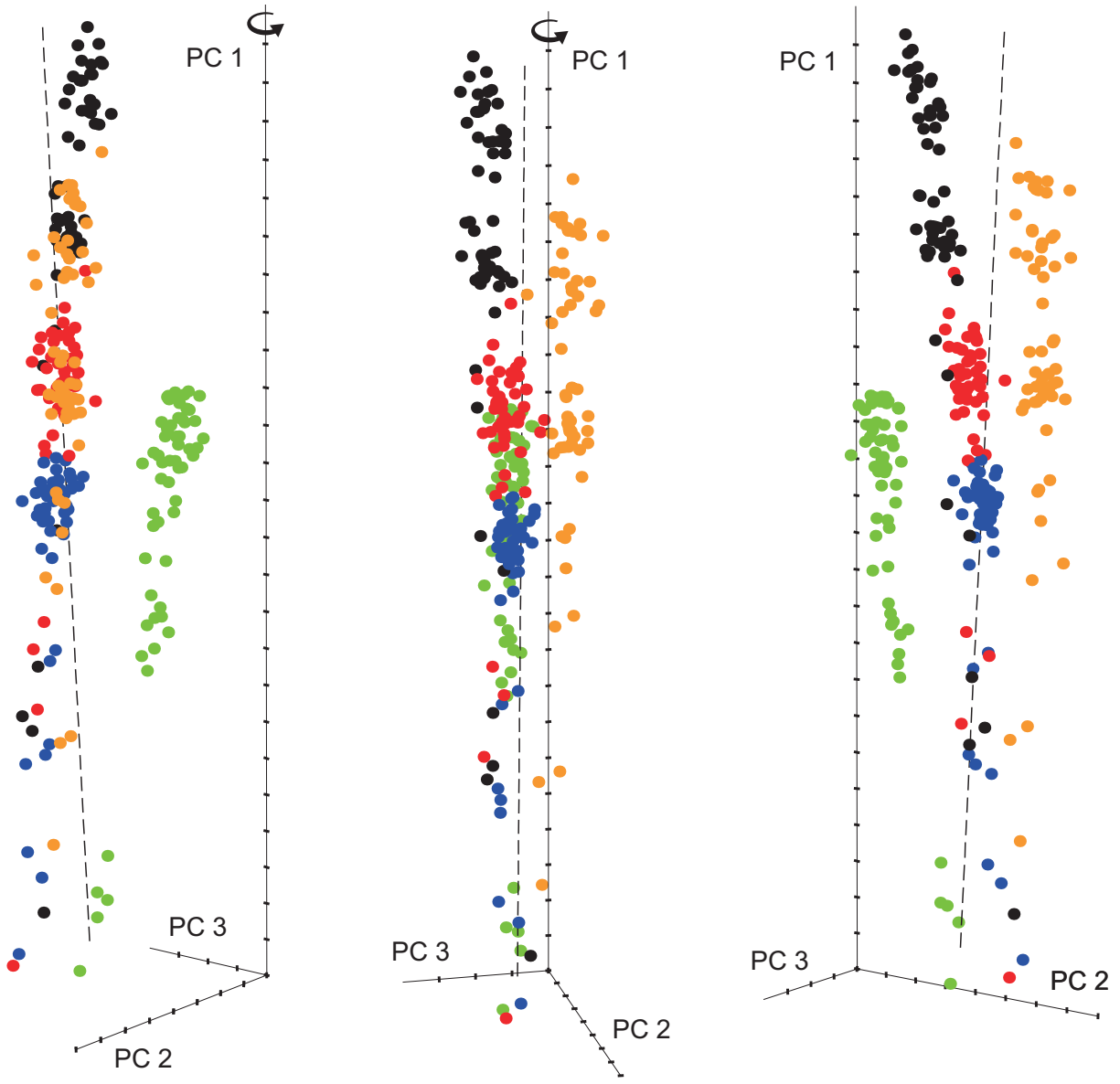

Fig. 6. Three different views of the first three principal components of size–shape space. The dashed line corresponds to the direction of pure size increase (see text). The relation of the ontogenetic trajectories depends on the projection onto the paper—the divergences are best visible in the third panel.

different and more or less diverging postnatal shape trajectories for cranial landmarks is also known for non-hominid primates (Richtsmeier et al., 1993; O'Higgins, 2000a,b; O'Higgins et al., 2001; Zumpano and Richtsmeier, 2003). Inasmuch as these ontogenetic trajectories are not parallel across species, neither in shape space nor in size–shape space, the pooled regression we used for common allometry (CAC) represents merely an average across the species here. This average is most similar in its geometry to the regression observed in our two samples of chimpanzees,

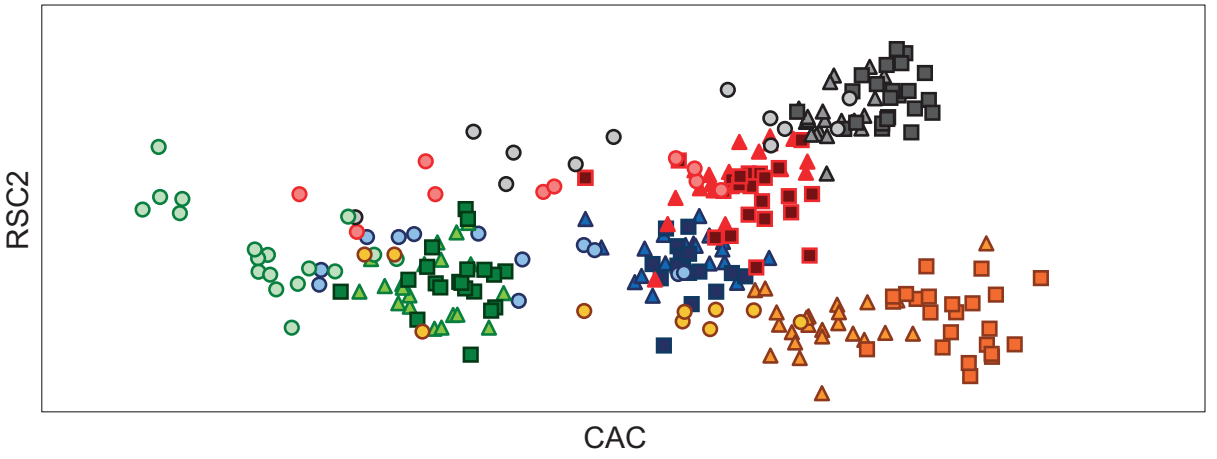

Fig. 7. A plot of CAC vs. an additional shape component (RSC2) shows a divergence of the African ape trajectories.

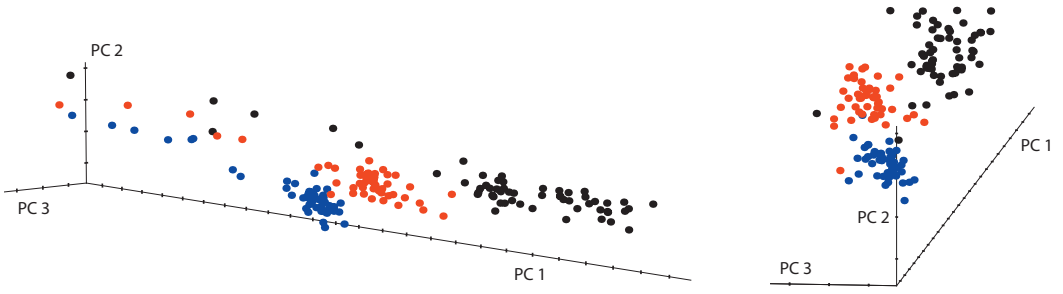

Fig. 8. Size–shape space for African Apes only. Left: A view showing the divergence during ontogeny; Right: A view perpendicular to the axes of allometry.

particularly that for bonobos. Notice, also, that bonobos lie quite close to the sample mean shape in the second and third of these principal dimensions. This could support older arguments from ecology, behavior, and other aspects of morphology that *Pan*, and especially the bonobo, comes closest to the great ape ancestor in its overall ontogenetic pattern (see e.g., Ciochon, 1983; Zihlman and Lowenstein, 1983; Susman, 1987; Zihlman et al., 1987). But we do not argue that least-squares methods have any particular competence for *estimating* ancestral states. Common allometry was calculated by a simple regression using the pooled covariance matrix; sampling of specimens and (sub)species, species-specific heteroscedasticity along the first PC, and phylogenetic covariance were not considered. We did, however, test whether the orientation of the common allometric component is influenced by the fact that *Pan* is the only genus with two species in our sample. We repeated the computation one time with bonobos dropped from the sample and another time with common chimpanzees dropped. In both cases CAC was aligned with the single species of *Pan*, showing that the orientation of CAC is not an artifact of the doubled weight of the genus *Pan*.

Recent geometric morphometric studies of chimpanzees and humans (Penin et al., 2002) or hominids (Ackermann, 2002; Bruner and Manzi, 2001) reported more or less parallel ontogenetic trajectories in shape space. These findings typically derive from data sets limited to higher ontogenetic stages or dental developmental stages than those

used here, and typically rely on fewer shape variables than the 288 of this study. When earlier postnatal stages are sampled and coverage of the craniofacial complex is richer, the nature of the findings fundamentally changes. We find that human craniofacial morphology is already markedly distinctive from the apes at birth, in accord with previous studies based on more traditional methods (e.g., Stark and Kummer, 1962; Dean and Wood, 1984). Non-human infants, however, are not separated according to species in our first three SSPC scores. That is, gross shape differences between *Homo* and the other hominids appear much earlier in ontogeny than those distinguishing the great apes. Evidently, the timing of *Homo*'s morphological divergence from some more primitive hominid developmental trajectory lies somewhere in the prenatal period. Indeed, until puberty, the *Homo* growth trajectory, perhaps driven by cerebral hypertrophy (reflected in the cranial base changes expressed in RSC1), is most steeply divergent from those of the other species in our sample; but then, strikingly, it becomes parallel to the common allometry just at the time of onset of sexual dimorphism. This change in the direction of development might correspond to the termination of brain growth that takes place particularly late in *Homo* (see e.g., Ulijaszek et al., 1998; Rice, 2001), the onset of puberty itself, and other associated processes.

In terms of the three hypotheses set out in our introduction, H_1—pure heterochrony—is obviously falsified because *Homo* does not share an ontogenetic trajectory with the other taxa. There could be more localized heterochronic processes responsible for the different trajectories, but this cannot be inferred from the present kind of overall analysis (Mitteroecker et al., in press). We also falsified H_2—namely a common point of divergence in hominid ontogeny. Instead, there is support in the data for H_3, an earlier divergence of the human growth trajectory from the common hominid allometry.

Several studies that analyze the ontogeny of the African apes find strong evidence for ontogenetic scaling along the lines of H_1 (Coolidge, 1933; Giles, 1956; Pilbeam and Gould, 1972; Gould, 1975; McHenry and Corruccini, 1981; Shea, 1983a,b, 1989, 1994). It is claimed that bonobos, common chimpanzees, and gorillas share a common allometric growth pattern to different extents, accounting for their differences in adult morphology. *Pan paniscus*—the pygmy chimpanzee—is regarded as retarded along this common growth relative to *P. troglodytes*, and *Gorilla* resembles an "overgrown" chimpanzee. Our Figs. 2, 4–6 illustrate that such scaling may indeed be responsible for a large amount of the shape variation among the African apes. But Figs. 7 and 8 show additional processes at work: the African apes are not pure allometric variants of one single type. Shape features uncorrelated with CAC, the direction of common growth, distinguish among the two chimpanzee species and gorillas along RSC2. By definition, differences in these RSC's that emerge during ontogeny are divergences from the common allometry.

Strand Vidarsdottir and Cobb (2003) stress that heterogeneous cross-sectional samples should be interpreted with caution because even the trajectories of different human populations differ very early in ontogeny (Strand Vidarsdottir et al., 2002). The inter-species differences of trajectories in our study, however, are clear enough to merit biological interpretation. More significantly, because we presented just three components of this five-species, 96-point sample, our interpretation is restricted to very general shape changes; because we grouped only by species, distinctions at lower taxonomic levels are not accounted for (but see the forthcoming manuscript on sexual dimorphism, Schaefer et al., in press). While we do not claim that *all* species differences among the African apes appear postnatally, for the gross shape components studied here this seems true.

The inconsistency of our results with the older literature arises mostly from our mode of analysis. While the conclusions of allometric scaling rest on bivariate scatters of selected size or length variables, the present study applies multivariate techniques. If some variables exhibit the same allometric relationships across species, but others do not, then overall allometry between the compared species is not identical (Godfrey and Sutherland, 1996; Klingenberg, 1996, 1998), and thus hypothesis tests for overall ontogenetic scaling or heterochrony models would need to be

multivariate. As the phenomenon of mosaic evolution and dissociated heterochrony is well documented, heterochrony should be studied on regional levels as well. In our view, no data analysis can be sufficient for that purpose that picks suitable variables a posteriori to fit the allometric scaling hypothesis. Similarly, the interpretation of single principal component scores along the lines of heterochrony, as suggested by Eble (2002), is flawed. Principal components are statistical constructions that combine different regions and thus can almost never correspond to actual biological factors. Instead, a sufficient number of principal components should be interpreted at once to understand the pattern of differences and divergences in an ontogenetic sample consisting of several species.

We have shown in this study that *Homo sapiens* craniofacial morphology is distinct from that in *Pan*, *Gorilla* and *Pongo* both in shape and in size–shape space. According to molecular studies *Homo* and *Pan* are more closely related than *Pan* is to *Gorilla* or *Pongo*. In ontogeny these form differences between *Homo* and the great apes appear much earlier than the differences that separate great apes among themselves. Genetic changes affecting early ontogeny can give rise to large morphological differences in adults. Our study shows that this may have been the case in the evolution of the human cranium. The small genetic differences between humans and chimpanzees affect early human cranial development and thus cause the extraordinarily distinct adult morphology. The genetic differences among the great apes—much larger than between *Homo* and *Pan*—have a later effect during ontogeny and therefore not as fundamental an impact on craniofacial morphology. Pure heterochrony does not sufficiently explain human craniofacial morphology nor the differences among the African apes.

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Appendix

The first part of the appendix offers the formulas for the ordination of shape space such that pooled allometry serves as first component and a PCA of the residuals as the subsequent components. The second part of the appendix presents the proof that the natural logarithm of centroid size extends shape space to size–shape space, and also explores the properties of principal components in this space. The matrix notation used in the appendix can directly be programmed in a mathematical package like Matlab or Mathematica. We apologize for the mathematical details in the proof, but apparently the proposition has not previously appeared in print.

Allometric analysis in shape space

The allometric model for dependence of an observed morphological measurement Y on a size factor X is taken in its linear version, $Y \sim a+bX$, rather than the loglinear version of Huxley, whether or not the dependent variables Y are scaled in the same unit as the size variable X.

Let $\mathbf{X}$ be the $n \times m$ matrix of shape coordinates after they have been group mean centered and let $\mathbf{s}$ be the $n \times 1$ vector containing the logarithm of centroid size (CS). The vector of the "common allometric component" is $\mathbf{a}=(\mathbf{X}^t\mathbf{s})/(\mathbf{s}^t\mathbf{s})$; we normalize it as $\mathbf{a}' = \mathbf{a}/\sqrt{\mathbf{a}^t\mathbf{a}}$. (The use of PC1 as allometric size applies only when the variables are size measures, but in this context we are restricted to shape coordinates only.) The subsequent components (RSC) should express a decomposition of the residual information. We project out the common allometric component to get a reduced data matrix

$\mathbf{W}=\mathbf{X}(\mathbf{I}-\mathbf{a}'(\mathbf{a}')^{t})$.

Decompose $\mathbf{W}^{t}\mathbf{W}$ as $\mathbf{V}\mathbf{D}_{W}\mathbf{V}^{t}$. Now the columns of $\mathbf{V}$ are residual components we seek with scores $\mathbf{XV}$. The first component $\mathbf{a}'$ is orthogonal to all subsequent components, and all scores $\mathbf{XV}$ are uncorrelated. The full set can be plotted as if one single set of principal components.

Allometric methods in size–shape space

The size–shape analyses in this paper are principal component analyses of a morphometric space constructed by adding one variable to the usual Procrustes shape coordinate formalism. It should not be confused with "form space" (Rohlf, 1996), a set of centered and rotated landmark coordinates in which there is no natural metric and no method like PCA. Size–shape space (Dryden and Mardia, 1998) is the extension of Procrustes space by one additional dimension of log CS. The resulting Euclidean metric is spherical on the hypothesis of pure digitization error, and thus this space does support interpretation of PC's.

We are asserting that "in the limit of small variations" (of both size and shape), the appropriate additional column to add to the Procrustes shape coordinate data matrix is the logarithm of Centroid Size (root sum squared distance of all the landmarks from their centroid case by case). The claim is equivalent to the assertion that in the complete absence of any meaningful biological signal, the analysis of this data matrix will yield no pattern (i.e., a spherical principal component structure). We are asserting, therefore, that on the so-called *offset isotropic Normal model* of small identically distributed independent variations at every landmark in every Cartesian direction separately, Centroid Size is (approximately) uncorrelated with every dimension of Procrustes shape space, and that the appropriate scaling of Centroid Size is by its logarithm.

For data in two dimensions, the first proposition was proved in Bookstein (1986) for one basis of shape space, the two-point (Bookstein) coordinates; it must necessarily remain true of the Procrustes shape coordinates or any other basis. It also follows from the zero entries in formula 8.9 of Dryden and Mardia (1998) for the approximate covariance of Centroid Size and shape in Kendall coordinates on the isotropic model. (The exact joint distribution is the subject of Corollary 8.3 in the same monograph.)

An alternate way to arrive at this approximation, valid for both two-dimensional and three-dimensional data, linearizes both Centroid Size and the Procrustes shape coordinates as subspaces of the full joint multivariate Gaussian distribution $X\sim N(\mu,\sigma^2 I_{dk})=\mu+Y$ for $Y=N(0,\ \sigma^2 I_{dk})$, d=2 or 3, where the mean form μ is centered (i.e., $1^{t}\mu=0$) and σ^2 is small with respect to the size of μ. Write Z for the vector that results from the perturbations Y after they themselves are centered dimension by dimension. Then, because $(x+z)^2\sim x^2+2xz$ for $z\ll x$, the Centroid Size of X is approximately the Centroid Size of μ plus the projection of the centered perturbations Z on the vector μ. Furthermore, the space of Procrustes shape coordinates is approximately the space of residuals of the original $2k$- or $3k$-dimensional distribution after 4 dimensions (for d=2) or 7 (for d=3) have been projected out: d dimensions for translation of the centroid, one dimension for Centroid Size itself, and 1 (d=2) or 3 (d=3) dimensions of rotation $\mu_k\otimes 1-1\otimes\mu_j$, $j\neq k$=1, …, d. Because all these directions of projection are mutually perpendicular, by Cochran's Theorem projections in the corresponding subspaces are independent; but that is already the first half of what we needed to prove.

There remains the issue of normalizing the dimension of Centroid Size (projection on μ) with respect to the subspace standing in for Procrustes shape. This is done by converting the projection along μ to a unit vector. But a projection on $\mu/\sqrt{\mu^{T}\mu}$ is equivalent to dividing each actual Centroid Size by grand mean CS. For any positive variable y of small variation, the derived variable $y/\bar{y}$ is nearly identical to the variable log y. Thus when the usual Procrustes shape construction, which is spherical in $2k-4$ or $3k-7$ dimensions, is augmented by one additional dimension of log Centroid Size, the approximate distribution remains spherical in $2k-3$ or $3k-6$ dimensions on the isotropic offset normal assumption.

The reader is encouraged to simulate isotropic variations around a general mean form in two or

three dimensions, compute Centroid Size and Procrustes shape coordinates, then produce the principal component structure of the size–shape spaces following this instruction. The resulting distributions should be spherical, without any pattern information.

For the data set at hand, let **S** be the $n \times (m+1)$ matrix $(\mathbf{s}|\mathbf{X})$. Decompose $\mathbf{S}^t\mathbf{S}$ as $\mathbf{U}\mathbf{D}_S\mathbf{U}^t$ where **U** is a matrix of eigenvectors and $\mathbf{D}_S$ a matrix of eigenvalues. Now the columns of **U** are the principal components of the size–shape space (SSPC) and **SU** are the corresponding scores. The first row of **U** contains the loadings for size, so that within a two- or three-dimensional PC plot a vector of pure size difference can be drawn along its direction. An SSPC is visualized by adding the 2 … $(m+1)$ elements of each column of **U** to an average shape configuration and scaling the resulting form by the antilog of the first entry in the column.

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